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New data on the diversity and distribution of lineages of the *Acanthodactylus erythrurus* species complex in North Africa derived from mitochondrial DNA markers

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Abstract

Patterns of morphological and genetic diversity within the fringe-toed lizards of the genus *Acanthodactylus* have puzzled systematists since the first assessments, and none more so than the *Acanthodactylus erythrurus* complex. A recent study combining multi-locus sequence data and morphological characters partially resolved the situation, identifying two new species in the southern part of the range in Morocco, but leaving an unresolved "Ibero-Moroccan" clade containing much of the genetic and morphological diversity. Here we sequenced a mitochondrial marker for new samples from across much of the distribution. Our data notably increase the known ranges of various species and lineages found in Morocco, and indicate a divergent genetic lineage within one of the newly described species. While far greater numbers of genetic markers will be needed to resolve taxonomic questions, greater geographic sampling is also still needed both to delimit the species, and to identify regions where potential genetic admixture may occur.

Key Words

Acanthodactylus lacrymae, *Acanthodactylus montanus*, NADH dehydrogenase subunit 4, phylogeography

Introduction

Acanthodactylus, or fringe-toed lizards, comprise the most specious genus within the family Lacertidae, with 44 recognized species (Uetz 2023). The genus is a member of the Eremiadini tribe within the subfamily Lacertini, which along with its phylogenetically closest members (including *Mesalina*; Garcia-Porta et al. 2019) primarily inhabits xeric habitats in North Africa and Asia (Sindaco and Jeremčenko 2008). *Acanthodactylus* ranges from the Iberian Peninsula, across North Africa and the Arabian Peninsula into western India, and northward to Turkey.

Acanthodactylus erythrurus (Schinz, 1838) is distributed across Morocco and Algeria and is the only species of the genus occurring in the Iberian Peninsula. It is usually found in habitats with a moderate supply of moisture in shrubland, mesic forests and rocky areas (Schleich et al. 1996). The Iberian Peninsula was colonized from North Africa (Harris et al. 2004), and the respective populations have shown high levels of admixture in their mitochondrial DNA (mtDNA), especially in the northern part of their distribution (Harris et al. 2019). Concerning the North African populations, *Acanthodactylus erythrurus* group is of great interest due to its unclear taxonomy and complex intraspecific relationships (Harris et al. 2004; Fonseca et al. 2009; Tamar et al. 2016; Beddek et al. 2018).

Intraspecific variation within *Acanthodactylus erythrurus* is extensive, and has led to notable differences in how

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studies have treated this. Salvador (1982) and Arnold (1983) accepted *A. e. lineomaculatus* and *A. e. belli* as the two subspecies occurring in North Africa, while Bons and Geniez (1995) added the subspecies *A. e. atlanticus* from the Atlas Mountains and suggested that *A. e. lineomaculatus* deserved specific status. On the other hand, Squalli-Houssani (1991) proposed that all Moroccan subspecies should be considered as one highly variable species with morphological differences reflecting adaptation to local habitats. Studies employing mtDNA sequences revealed that both the Tunisian *A. blanci* and *A.* (*e.*) *lineomaculatus* are nested within the *A. erythrurus* complex (Harris et al. 2004; Fonsesca et al. 2009; Tamar et al. 2016). A comparative phylogeographic study based on mtDNA data, including samples of *A. erythrurus* and *A. blanci* from Algeria, revealed considerable mtDNA diversity within the species, with one species-delimitation approach (Automatic Barcode Gap Discovery, ABGD; Puillandre et al. 2012) indicating potentially 15 taxonomic units, the most of any of the species examined (Beddek et al. 2018). At the same time, a strong East-West divergence pattern across the Maghreb was identified, with two main clades showing this motif with a third basal clade reported only from the southern Atlas Mountains.

Some taxonomic issues regarding the *A. erythrurus* complex were resolved by Miralles et al. (2020), employing multilocus sequence data and a morphological assessment. They recovered five major lineages, that were supported by both mtDNA and nuclear DNA (nDNA). They continued to find a complex pattern across most of an Ibero-Moroccan (IM) clade, with highly diverse mtDNA lineages that did not fully coincide either with the three subspecies accepted in Morocco, or with nuclear markers. However, in the Atlas Mountains of Morocco two divergent lineages were identified in both mtDNA and the nuclear markers, which also showed minimal differences with some morphological characters, and these were recognized as distinct species, *Acanthodactylus montanus* from the High Atlas Mountain region and *Acanthodactylus lacrymae* from the Middle Atlas region. These were more closely related to Algerian and Tunisian forms rather than the Ibero-Moroccan clade (Miralles et al. 2020). These authors also highlighted the need for further sampling to better assess the distribution of these forms. Rancilhac et al. (2023) attempted to resolve the situation within the IM clade of *A. erythrurus* using mtDNA and nine nuclear gene fragments. However, even with this enlarged dataset they were only able to distinguish four major groups of populations, separated by barriers to gene flow. A recent genome-wide RADseq approach to investigate a contact zone within the IM clade indicated that there was spatial restricted gene flow highlighting high levels of reproductive isolation, consistent with even more species-level diversity within the complex (Doniol-Valcroze et al. 2024).

To obtain new insights into the distribution of the different lineages and species of the *A. erythrurus* complex, here we sequenced a partial ND4 mitochondrial gene region for 42 individuals, primarily from Morocco. Since mitochondrial and nuclear DNA were completely congruent for *A. montanus*, *A. lacrymae*, and the major lineages within the *A. erythrurus* complex (Miralles et al. 2020), this should give additional information regarding the distribution of these species, and also help delimit the ranges of mtDNA lineages within the rest of the *A. erythrurus* complex.

Material and methods

We analyzed 42 samples of *A. erythrurus* (Table 1). Animals were caught in the field over a 20-year period, and a small piece of tail tissue was removed before releasing them at the collection site. Locations and codes of the samples are represented in Fig. 1. Since lineages

Table 1. List of samples sequenced for this study.

Figure Code	Specimen number	Coordinates (Latitude, Longitude)
1	DB20115	31.4417, -9.7178
2	DB11946	31.4934, -9.7683
4	DB3661	32.6030, -9.1916
5	DB365	34.2044, -6.5619
6	DB1605	35.1659, -6.1209
7	DB3386	35.0225, -5.2044
8	DB3641	35.0626, -5.1950
9	DB3642	35.0626, -5.1950
11	DB3640	35.0626, -5.1950
14	DB4832	33.9447, -5.0279
15	DB15522	33.6521, -5.0226
16	DB15524	33.4085, -5.1082
17	DB15525	33.4085, -5.1082
18	DB14962	33.4085, -5.1082
19	DB14507	33.4085, -5.1082
20	DB25360	33.4056, -5.1030
21	DB1533	33.6218, -4.9034
22	DB949	33.1590, -5.0638
23	DB23755	33.1124, -5.0277
24	DB1015	31.8018, -5.4669
25	DB78	32.2164, -5.5497
26	DB81	32.1964, -5.6429
27	DB91	32.1964, -5.6429
28	DB95	32.1964, -5.6429
29	DB134	32.1964, -5.6429
30	DB137	32.2164, -5.5497
31	DB3628	32.1964, -5.6429
32	DB1512	31.9697, -5.4879
33	DB915	31.2908, -7.3814
34	DB1461	30.7880, -7.5935
35	DB24038	32.5694, -3.7186
36	DB24128	32.5694, -3.7186
37	DB24136	32.5694, -3.7186
38	DB24158	32.5694, -3.7186
39	DB24160	32.5694, -3.7186
40	DB14625	33.8653, -3.0323
41	DB3647	33.8724, -3.0387
42	DB3648	33.8724, -3.0387
43	DB3654	33.8724, -3.0387
44	DB3655	33.8724, -3.0387
45	DB14453	33.8653, -3.0323
48	DB11221	35.293, 1.2631

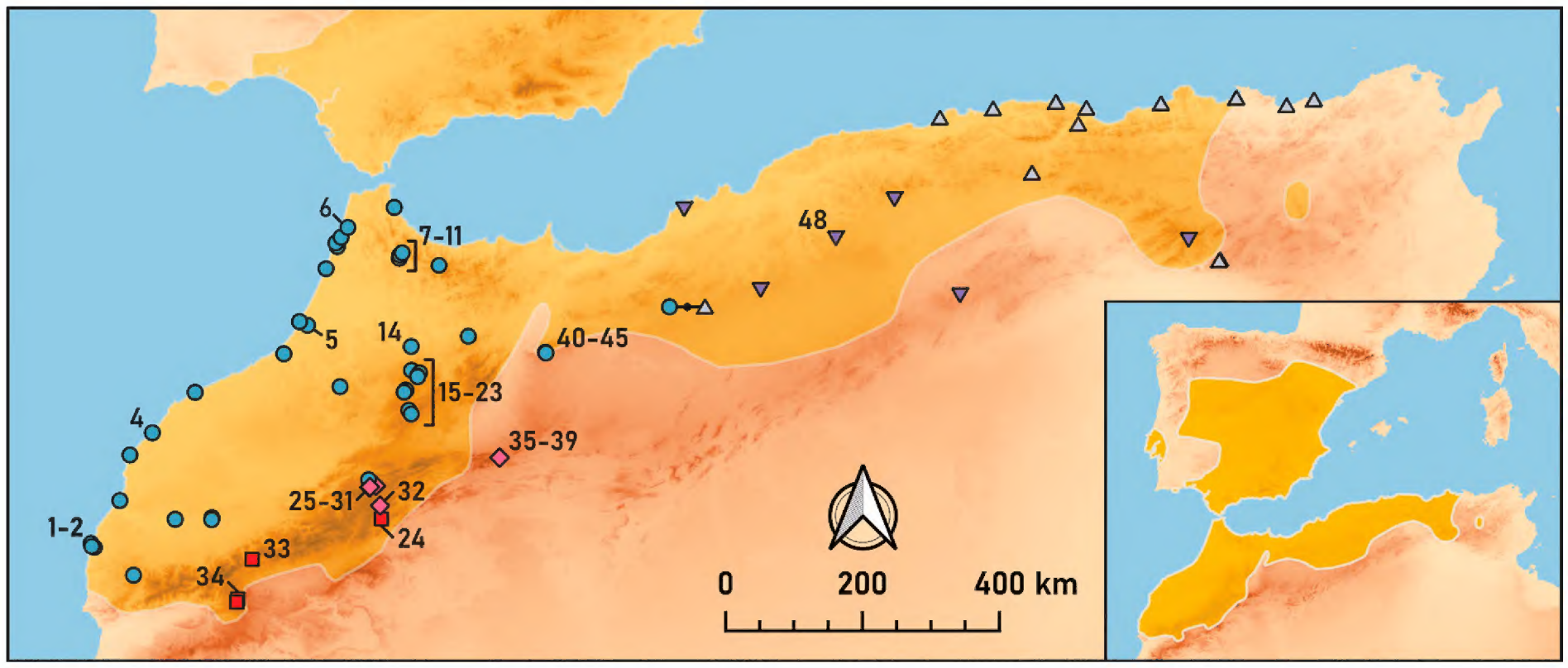

Figure 1. Distribution map of lineages within the *Acanthodactylus erythrurus* complex within North Africa with complete range inset. Distribution outline follows the IUCN. Newly sequenced individuals in this study are numbered, others are from GenBank. Colour codes indicate the different forms – *A. erythrurus* complex IM clade (blue circles), *A. montanus* (red squares), *A. lacrymae* (pink diamonds), *A. erythrurus* complex Central Algeria Clade (purple triangles), *A. erythrurus* complex Algero-Tunisian clade (light blue triangles).

and species cannot always be determined with certainty based on morphological characters of single individuals (see Miralles et al. 2020), all individuals were sequenced. Additional data from previous studies were retrieved from GenBank (Tamar et al. 2016; Beddek et al. 2018; Miralles et al. 2020) covering the distribution range of the species. Sequences of *A. micropholis*, *A. blanfordii*, *A. grandi* and *A. boskianus* (Heidari et al. 2014) were included as outgroups. All new sequences were submitted to GenBank (PQ000925–PQ000966).

Total genomic DNA was extracted from alcohol-preserved tail tissue following standard high-salt protocols (Sambrook et al. 1989). We amplified a mitochondrial gene fragment, NADH dehydrogenase subunit 4 gene with the adjacent tRNAs (ND4+His, Ser, Leu) in order to allow comparison with previous published studies of *A. erythrurus* using this marker (Tamar et al. 2016; Beddek et al. 2018; Miralles et al. 2020). The fragment was amplified performing a Polymerase Chain Reaction (PCR) with primers ND4 and Leu from Arévalo et al. (1994), in a total volume of 25 µl, with 5 µl of 5x reaction Buffer, 3.2 µl of 25 mM $MgCl_2$, 1 µl of 5 mM dNTPs, 0.5 µl of 4.0 M of each primer, and 0.2 µl (1U) of Promega GoTaq DNA polymerase. PCR conditions were: pre-denaturation step of 94 °C (3 min), 33 cycles with 94 °C (30 s) denaturing, 47 °C (40 s) annealing, 72 °C (90 s) extension and with a final extension conducted at 72 °C for 5 min. Positive PCR products were sent to GENEWIZ (Germany) for sequencing.

Sequences were edited and aligned using ClustalW with default parameters in MEGAX (Kumar et al. 2016). Genetic uncorrected *p*-distances were also calculated in MEGAX (Kumar et al. 2016).

We employed two methods of phylogenetic inference based on the ND4 sequences, Maximum Likelihood (ML) and Bayesian Inference (BI). Best-fit partition schemes were selected using Partition Finder v1.1.1 (Lanfear et al. 2012). We used codon partitions and the tRNAs fragment was set as a fourth data block. ML analysis was performed with MEGAX with the built-in tool to choose the most appropriate model under the AIC (GTR+G), while nodal support was assessed by bootstrapping with 5,000 replicates. The BI analysis was carried out using MrBayes v3.2.7 (Ronquist et al. 2012) and separate models were set for the different partitions (in each case GTR+I+G). Two independent runs of 5×10^6 generations were performed, with a sampling frequency of 1,000 and 25% of the trees were discarded as burnin. Trees were imported to FigTree v1.4.4 for visualization.

Results

The dataset consisted of 42 newly sequenced members of the *A. erythrurus* complex, along with 105 previously published sequences from GenBank, with an aligned length of 769 bp. Both Bayesian Inference and Maximum Likelihood analysis for the mitochondrial fragment (ND4) produced almost identical topologies, differing slightly in the deeper nodes, with the BI tree revealing higher support on some nodes (Fig. 2). Our results are generally congruent with previous studies regarding the major clades (Beddek et al. 2018; Miralles et al. 2020). Following the taxonomy of Miralles et al. (2020), all five major clades – the species *A. montanus* (WHA) and *A. lacrymae* (EHA), the highly diverse Ibero-Moroccan (IM) clade, the Algero-Tunisian clade (AT) and the Central Algerian clade (CA) can all be identified (Fig. 2). However, when comparing the distribution of these clades (Fig. 1) with the newly sequenced specimens for this study there are

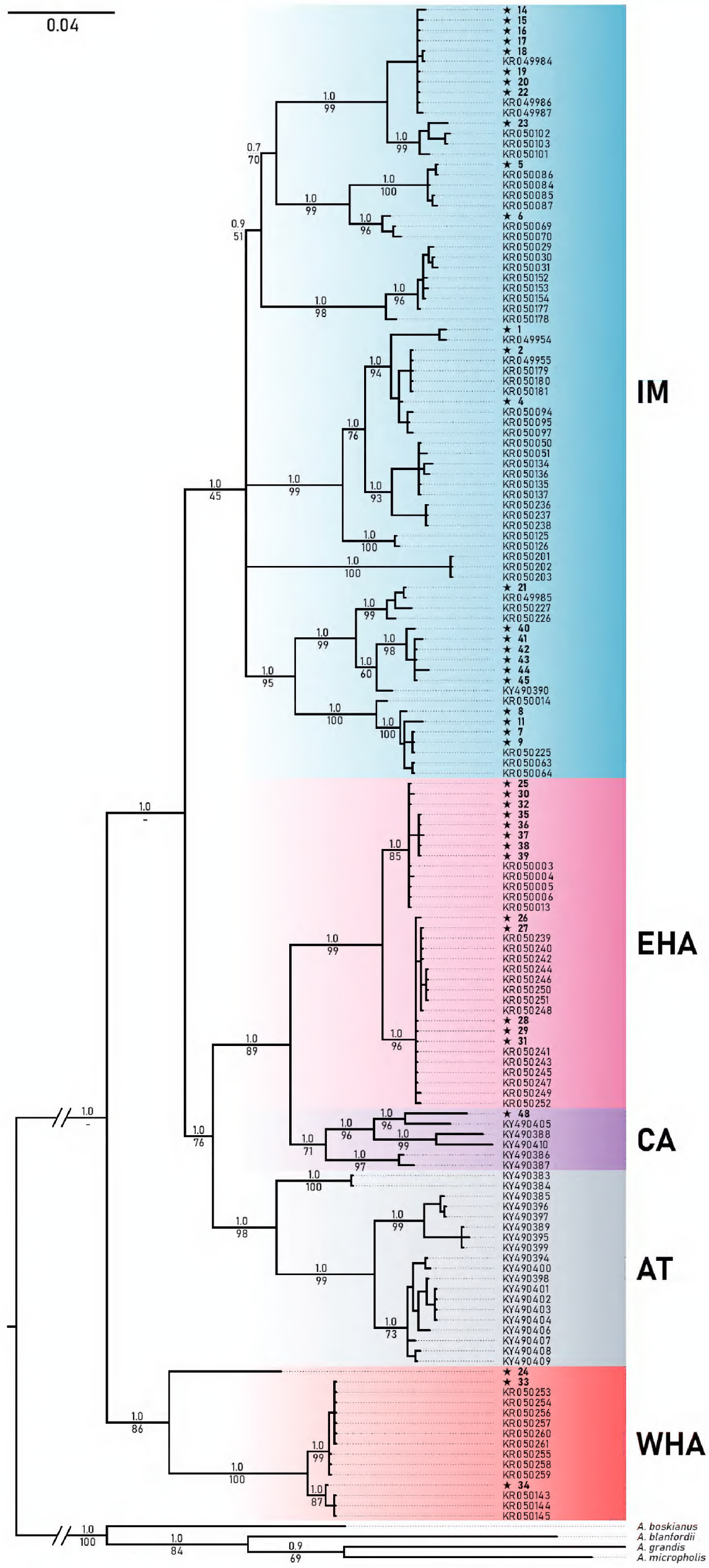

Figure 2. Estimate of relationships within the *A. erythrurus* complex in North Africa derived from a Bayesian analysis. Lineages are labelled following Miralles et al. (2020): *A. erythrurus* complex Ibero-Moroccan clade (IM), *A. montanus* (WHA), *A. lacrymae* (EHA), *A. erythrurus* complex Central Algeria Clade (CA), *A. erythrurus* complex Algero-Tunisian clade (AT). Stars indicate novel samples from this study, and numbers above and below nodes indicate Bayesian Posterior Probabilities and Bootstrap support from a Maximum Likelihood analysis respectively. Missing Bootstrap support values are due to different placement of the WHA clade with Maximum Likelihood, where it appears as sister-clade to EHA, CA, and AT.

some notable modifications. Regarding the IM clade, our new sequences from Debdou (Fig. 1: 40–45) fills a wide gap in sampling for this clade, which had previously been confirmed around the region of Taza and then a single sample over 200 km to the East in Algeria (Fig. 1). For *A. lacrymae*, our samples from just north of Aït Aïssa (Fig. 1: 35–39), extend the range over 100 km to the East of the previously confirmed populations. For *A. montanus* our sample 24 (Fig. 1) not only increases the apparent range of this lineage about 200 km to the northeast, it also means that the ranges of *A. montanus* and *A. lacrymae* can no longer be considered highly allopatric, since they are separated by at most around 10 km. This sample 24 is also interesting genetically, as although it is strongly supported as sister taxa to *A. montanus* (97% BPP), it is highly distinct from the samples from the southern part of the range (samples 33–34, 8±1% SE).

Discussion

Just as early assessments of morphological variation within the *A. erythrurus* complex identified high levels of complexity (Salvador 1982; Arnold 1983), so later assessments of genetic diversity have continued to perplex researchers. Miralles et al. (2020) managed to describe two species from the southeastern edge of the range, *A. lacrymae* and *A. montanus*, while leaving the bulk of the morphological and genetic diversity within an unresolved *A. erythrurus* IM clade. Our additional sampling further supports the distribution of this latter clade, across the Moulouya river valley region in Debdou, with these most closely related to a single published sequence from even further east (KY490390, Beddek et al. 2018), that indicates the IM clade reaches into Algeria (Fig. 1). The Moulouya region is often considered a biogeographical barrier separating herpetofauna into western and eastern forms (reviewed in Salvi et al. 2018), and the samples from the East of the Moulouya valley do form a subgroup within the IM clade, again highlighting the intricacy of the phylogeographic patterns within the *A. erythrurus* complex (Rancilhac et al. 2023).

Regarding the situation in the Atlas Mountains and the southeastern range of the distribution, Miralles et al. (2020) recognized *A. montanus* and *A. lacrymae* for the two highly genetically distinct lineages they recovered in this region. While these two forms can be morphologically separated from the IM clade of the *A. erythrurus* complex, Miralles et al. (2020) noted that *A. montanus* is "very similar to the allopatric *Acanthodactylus lacrymae* and single individuals are not always possible to separate". However, the situation was simplified by the large distance between the ranges of the species – indeed these authors specifically presented networks of nuclear haplotype sharing between both *A. montanus* and *A. lacrymae* with the IM clade, but not between *A. montanus* and *A. lacrymae* (fig. 5 of Miralles et al. 2020). The finding of a distinct lineage apparently of *A. montanus* very close to the range of *A. lacrymae* (sample 24; Fig. 1) complicates this situation. Since these species cannot be easily separated in the field, extensive genetic sampling of individuals from the region of contact between *A. montanus* and *A. lacrymae* will be needed to confirm if there is genetic admixture, or if the two lineages are found in strict sympatry. Furthermore, the high degree of genetic differentiation between this sample (24) and *A. montanus* from the type locality (8% with this ND4 marker) is higher than between some accepted lacertid lizard species (e.g. *Dinarolacerta mosorensis* and *Dinarolacerta montenegrina*; 6.7%, Mendes et al. 2016). On the other hand, divergence levels were similar (7.8%) within another lacertid, *Timon tangitanus*, in Morocco which showed a lack of lineage sorting with nuclear markers (Abreu et al. 2020). While Rancilhac et al. (2023) were unable to fully delimit sublineages within the IM clade based on multiple nuclear markers, recent analyses of RADseq genome-wide data indicate that some of these at least correspond to cryptic species (Doniol-Valcroze et al. 2024). A similar approach will probably be needed to determine the taxonomic status of this new lineage.

To conclude, phylogeographic patterns within the *A. erythrurus* complex continue to slowly take shape. Our additional geographic sampling extends the ranges of some forms found in Morocco, the *A. erythrurus* IM clade, *A. montanus* and *A. lacrymae*. In particular, a genetically distinct apparent individual of *A. montanus* was found very close to the known range of *A. lacrymae*. Determination of genetic admixture between *A. montanus* and *A. lacrymae* will be necessary to confirm the genetic distinctiveness of these morphologically extremely similar forms. Our data highlights that, as well as the previously identified need for inclusion of greater numbers of genetic markers or even genomic level assessments (Doniol-Valcroze et al. 2024), increased geographic sampling is also needed, especially across the southeastern part of the range in Morocco where the distribution of the different species and lineages is still not fully determined.

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